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A Bayesian Random Effects Discrete-Choice Model for Resource Selection: Population-Level Selection Inference

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Abstract

*Modeling the probability of use of land units characterized by discrete and continuous measures, we present a Bayesian random-effects model to assess resource selection. This model provides simultaneous estimation of both individual- and population-level selection. Deviance information criterion (DIC), a Bayesian alternative to AIC that is sample-size specific, is used for model selection. Aerial radiolocation data from 76 adult female caribou (*Rangifer tarandus*) and calf pairs during 1 year on an Arctic coastal plain calving ground were used to illustrate models and assess population-level selection of landscape attributes, as well as individual heterogeneity of selection. Landscape attributes included elevation, NDVI (a measure of forage greenness), and land cover-type classification. Results from the first of a 2-stage model-selection procedure indicated that there is substantial heterogeneity among cow-calf pairs with respect to selection of the landscape attributes. In the second stage, selection of models with heterogeneity included indicated that at the population-level, NDVI and land cover class were significant attributes for selection of different landscapes by pairs on the calving ground. Population-level selection coefficients indicate that the pairs generally select landscapes with higher levels of NDVI, but the relationship is quadratic. The highest rate of selection occurs at values of NDVI less than the maximum observed. Results for land cover-class selections coefficients indicate that wet sedge, moist sedge, herbaceous tussock tundra, and shrub tussock tundra are selected at approximately the same rate, while alpine and sparsely vegetated landscapes are selected at a lower rate. Furthermore, the variability in selection by individual caribou for moist sedge and sparsely vegetated landscapes is large relative to the variability in selection of other land cover types. The example analysis illustrates that, while sometimes computationally intense, a Bayesian hierarchical discrete-choice model for resource selection can provide managers with 2 components of population-level inference: average population selection and variability of selection. Both components are necessary to make sound management decisions based on animal selection. (JOURNAL OF WILDLIFE MANAGEMENT 70(2):404–412; 2006)*

Key words

Bayesian, caribou, discrete-choice, habitat, random effects, resource selection.

A common resource-selection study design uses locations of uniquely identified individual animals recorded over time (e.g., via radio or Global Positioning System [GPS] collars) to describe habitat use. Attributes (e.g., land-cover types, elevation) of used locations are compared to those collected at available locations to assess selection. Animal locations are assumed to be far enough apart in time to be considered independent, and availability is treated as known and equal for all animals. Thomas and Taylor (1990) categorize this type of study design as a Design 2 study.

Design 2 studies provide data for assessing resource selection for individual animals and at the population level by examining selection across animals. For example, individual selection of categorical habitat types may be assessed using a chi-square statistic (Neu et al. 1974) and population-level selection assessed using the sum of individual chi-squares (White and Garrott 1990) or a maximum chi-square statistic (Dasgupta and Alldredge 1998, 2000, 2002). However, these methods do not assess whether individual animals are selective in the same way. Thus, if use is random at the population level with half the animals using a resource less than its availability and half using the resource more than its availability to the same degree, these methods will lead researchers to infer population-level selection when none exists. Evidence of individual selection across a group of individuals is

not evidence for population-level selection unless the direction of individual selection is relatively consistent.

For continuous variables describing resource units, some researchers average individual parameter estimates across animals to estimate population-level selection parameters. Glenn et al. (2004) fit a logistic-regression model to each animal and reported mean estimated parameter coefficients across animals to describe population-level selection. This approach assesses population-level selection because opposite choices by animals would result in an inference of no population-level selection. However, if the numbers of relocations differ among animals, this approach averages estimates without accounting for their differing standard errors and thus yields an incorrect error estimate for assessing population-level selection. As a result, animals with few observations and less precise parameter estimates disproportionately impact the mean value. Miller et al. (2000) avoided this problem in their use of a single logistic regression across animals by using a random sample of 10 locations/animal to "...prevent individuals monitored disproportionately from overly influencing estimated parameters." However, as a result, they did not use all of their relocation data to assess selection.

Random-effect models provide a mechanism to appropriately weight relocations and individuals that provide inferences for population-level selection using valid error terms. Several areas of ecology have employed random effects (also called hierarchical) models to describe natural processes. These include capture-recapture modeling (e.g., Johnson and Hoeting 2003, Burnham

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and White 2002, Brooks et al. 2000), modeling spatial distributions of species (Penttinen et al. 2003) and predicting invasive species population growth (Wikle 2003). The recent development of computational techniques such as Markov Chain Monte Carlo (MCMC; see Gelman et al. 2004) provides a relatively straightforward method to incorporate random effects into generalized linear models. Bernardo and Smith (1994) provide a theoretical treatment of the subject.

Bayesian methods are increasingly used for decision making in natural resource issues (Boyce 2002, Link et al. 2002). Thomas et al. (2004) presented a Bayesian model for categorical resource selection with known availability and illustrated analyses for each animal and across all animals. They identified several advantages of these methods including credible intervals (a Bayesian alternative to confidence intervals) and model-selection methods that are sample-size specific and do not rely on large sample theory. Also, credible intervals do not yield negative lower bounds and zero use of a given resource results in a meaningful interval for selection that is sample-size dependent. Their model is also relatively insensitive to the inclusion and exclusion of habitats. That is, selection inferences tend to not change if a habitat is dropped or added in the analysis.

Discrete-choice models, commonly employed in consumer selection studies in business and economics (Manski and McFadden 1981), have been used to assess resource selection by animals (Cooper and Millsaugh 1999; McCracken et al. 1998; Manly et al. 2002: chapter 8). Ramsey and Usner (2003) used a discrete-choice model with random effects to model individual heterogeneity in categorical habitat selection of bears. This model assumes that variability in selection among animals is constant across habitat types. In addition, Ramsey and Usner (2000) used a discrete-choice model with a persistence parameter to model the tendency of bears to stay in the same habitat type between successive relocations. They were not successful in fitting a single random-effects model with a persistence parameter. Dailey et al. (2007) examined habitat selection by trout with a Bayesian discrete-choice model with a seasonal persistence parameter.

We formulate a general Bayesian random-effects discrete-choice model for Design 2 (Thomas and Taylor 1990) resource-selection data for independent relocations of a collection of animals. We illustrate this model using caribou calving ground selection data using a mix of continuous and categorical variables characterizing plots of land.

Study Area and Methods

In this section, we describe an example data set, present the details of a Bayesian random-effects model, discuss inferences, and describe model-fitting and assessment details. The example data set is a subset of a long-term study comprised of 19 years of caribou locations (Griffith et al. 2002). Thus, the analysis presented here is for the purpose of illustrating estimation and assessment of sources of variation using random-effects models rather than serving as a treatise on caribou calving ground selection.

Caribou Calving Ground Data

Aerial relocations were obtained from 76 VHF radiocollared female caribou calves on the north slope of Alaska, USA, in June

1994. Calves were hand-captured within 2 days of birth during 1–3 June. Calves with cows were relocated daily, weather permitting, through 24 June. Locations were recorded with GPS; comparison to a local differentially corrected base station suggested that 95% of recorded locations were within 200 m of actual locations. The number of relocations per animal ranged from 3 to 22 with 75% of animals having at least 16 relocations (median = 18.00, mean = 16.70), resulting in 1,269 relocations. We generated daily, population level, 99% utilization distributions (UD, the area expected to include 99% of locations of all animals in the target population, all else held equal) with least-squares-cross-validated fixed kernels (Seaman and Powell 1996; Seaman et al. 1998, 1999), overlaid all these daily contours, and obtained the outer perimeter of all daily 99% UD's. An 8-km² habitat grid was generated, and the 131 cells within or intersecting the outer perimeter of daily 99% UD's was used as our available area for all individuals. No analyzed relocations occurred outside this available area. Thus, we estimated within-calving-ground habitat selection.

Three habitat attributes of each grid cell were considered: 1) continuous-elevation data obtained from 60-m² resolution Digital Elevation Models, 2) 6 categorical land-cover classes derived from a supervised classification of 30-m² resolution Thematic Mapper and 50-m² resolution Multi-Spectral Scanner images (Jorgensen et al. 1994, 2002; Griffith et al. 2002), and 3) continuous relative green plant biomass estimated with 1-km² resolution Normalized Difference Vegetation Index (NDVI; Tucker 1979, 1986) for 21 June (Griffith et al. 2002) derived from Advanced Very High Resolution Radiometer (AVHRR) data from National Oceanic and Atmospheric Administration (NOAA) polar-orbiting satellites. The three original habitat layers were resampled with ARCINFO to 8-km² resolutions using the zonal median for elevation and NDVI and the zonal majority for land-cover class. Land-cover classes were: 1) Wet Sedge, 2) Moist Sedge, 3) Herbaceous Tussock Tundra, 4) Shrub Tussock Tundra, 5) Alpine, and 6) Sparsely Vegetated. Attributes for grid cells that were only partly in the UD were determined for the entire cell or only for the portion that was not ocean. Our models use standardized Elevation (EZ) and NDVI (NZ) and 5 indicator variables for land-cover class (LC). Because previous work (Griffith et al. 2002) suggested that caribou selected areas within calving grounds based on NDVI and they typically calved between the coast (sea level) and the foothills in this area, we included linear (EZ, NZ) and quadratic terms (EZ², NZ²) for standardized elevation and NDVI to determine optimal levels of these attributes. We did not include snow-cover as a habitat attribute because the calving ground was snow-free at calving in 1994. Neither did we include the rate of change in NDVI as a habitat attribute because previous analyses (Griffith et al. 2002) showed that caribou did not select this attribute within annual calving grounds.

Bayesian Random-Effect Model Data Analysis

Bayesian random-effect (or hierarchical) models are typically composed of 3 parts: a data (likelihood) model, a parameter model, and a hyperparameter model. The data model commonly represents the likelihood used in traditional maximum-likelihood analysis. Similar to Manly et al. (2002), Barmi and Pontius (2000),

and Aebischer et al. (1993), we model the probabilities of use of grid cell s by animal i as

$$p_i(s) = \frac{e^{x(s)\beta_i} a_i(s)}{\sum_{r \in S} e^{x(r)\beta_i} a_i(r)}, \quad (1)$$

where $s \in \{1, 2, 3, \dots, 131\}$ is a grid cell, $x(s)$ is a k -dimensional vector of attributes characterizing grid cell s ; e.g., NZ, EZ, and LC2, LC3, LC4, LC5, LC6 (5 indicators with wet sedge as the reference type), $a_i(s)$ is the relative availability of grid cell s to animal i , and $\beta_i = (\beta_{i1}, \beta_{i2}, \dots, \beta_{ik})'$ is a k -dimensional vector of parameters for animal i . We considered all grid cells to be equally available to all caribou so $a_i(s) = 1/131$ and the model reduced to the discrete-choice model (McCracken et al 1998),

$$p_i(s) = \frac{e^{x(s)\beta_i}}{\sum_{r \in S} e^{x(r)\beta_i}}. \quad (2)$$

The parameter vector, β_i , of this model will be different for each animal so the probability of use of each grid cell may differ for each animal. No intercept term was included in the parameter vector β_i because it would have canceled with the same term in the denominator of $p_i(s)$ and inclusion of such a term might have led to convergence problems in Bayesian estimation.

For the j th independent relocation of animal i , the probability that location occurs in grid cell s_{ij} is $p_i(s_{ij})$. Thus, for m animals acting independently and n_i independent relocations of animal i , the likelihood for all recorded relocations is

$$\prod_{i=1}^m \prod_{j=1}^{n_i} p_i(s_{ij}). \quad (3)$$

This likelihood could alternatively be written as the product of m multinomial probabilities (see Ramsey and Usner 2003) if the number of relocations in each grid cell by each animal is summarized.

In models allowing individual effects, it is usually not the parameters in the individual models that are of interest. Rather, it is the parameters of a population-level model that generates these individual parameters that is the inferential target. The collection of estimated parameters across individuals is used to illustrate variation in selection and investigate differences among various subcollections of animals (e.g., gender, age class). In the parameter model, a selection model for each caribou represents a sample from a population of such models. Therefore, a probability model for the individual parameters (or random effects) is added to represent the random selection of caribou from a larger population. Here, the parameter models were taken to be $\beta_{il} \sim N(\beta_l^*, \sigma_l^2)$, for $l = 1, 2, \dots, k$. That is, we use independent normal distributions with common coefficient β_l^* and variance σ_l^2 to model individual selection parameters for all animals. β_l^* and σ_l^2 are commonly referred to as hyperparameters in the random-effects model. Estimation of the β_l^* provides inference concerning population-level selection based on resource attributes, and estimation of σ_l^2 allows description of the variability in selection across animals for each resource attribute.

The full likelihood of the random-effects model used, for example, to perform maximum-likelihood estimation for the hyperparameters and make population-level selection inferences requires integration of the data model times the parameter model

over the random effects. This integration typically leads to an intractable expression unless a conjugate parameter model is used (see Ramsey and Usner 2003). Our model differs from that of Ramsey and Usner (2000) in 2 key ways. First, we model the probability of use of a piece of land, s , characterized by attributes $x(s)$, by individual animals, not the probability of use of categorical habitat types by individual animals. Thus, while Ramsey and Usner modeled probability of use of 5 habitat types, we model the probability of use of 131 grid cells. Second, our model allows variability in selection among animals associated with an attribute to differ by attribute. For example, there may be more variability among animals in the selection of elevation than in greenness. The heterogeneity model of Ramsey and Usner assumed the variability in selection among animals associated with habitat types to be the same for all habitat types. Because of the greater generality of our model, a conjugate parameter model, like the Dirchelet parameter model used by Ramsey and Usner, was not used. Aitchison (1986) suggested that the Dirchelet parameter model unnecessarily limits the richness of the model, so Bayesian estimation was employed.

Bayesian methodology requires a prior distribution for all parameters in the model. Thus, the third part of the model is a prior distribution for the hyperparameters (sometimes called hyperpriors). Independent normal distributions with mean 0 and variance 100 were used here for the prior for each of the k β_l^* parameters and independent inverse-gamma distributions with parameters 0.01 and 0.01 (parameterized such that the mean is 1) for each of the k σ_l^2 . Our choices of priors result in vague prior information because large variances equal to 100 reflected the limited knowledge we possessed concerning the value of these parameters.

WinBUGS software, commonly used for Bayesian analysis of statistical models (Link et al. 2002), was used to fit our models (see <http://www.mrc-bsu.cam.ac.uk/bugs/>; Spiegelhalter et al. 1999, Gilks et al. 1994). Our programming approach was based on hierarchical centering, which improves the efficiency of estimation (Chen et al. 2000). An illustration of the data format and the WinBUGS program are provided in Appendices A and B, respectively.

Fitted models yield precisely estimated posterior distributions and Bayes estimates (means of these posterior distributions) for the population-level selection parameters, β_l^* , individual selection parameters, β_{il} , and the variability in selection among animals for each covariate, σ_l^2 . The Bayesian Output Analysis (BOA) package in R (R Development Core Team 2004) was used to obtain 95% highest probability density (HPD)-credible intervals (Chen et al. 2000:219) for β_l^* . WinBUGS was also used for model selection by determining the values of the deviance information criterion (DIC; defined in Appendix C), a Bayesian alternative to Akaike Information Criterion (AIC; see Burnham and Anderson 2002 or Spiegelhalter et al. 2002). Models with DIC values differing by ≥ 5 were considered substantially different in their fit to the data.

Bayesian model-fitting details in wildlife research are discussed thoroughly by Link et al. (2002), including the total number of iterations and chains to use; the number of burn-in iterations needed; and the purpose of thinning and convergence criteria (see also Gelman et al. 2004). We used 30,000 iterations in a single chain with the first 10,000 iterations used as a burn-in for parameter convergence. Thus, posterior distributions, parameter estimates, and DIC values are based on 20,000 iterations. The history plot of

model deviance across burn-in iterations confirmed convergence, and the Geweke (1992) convergence diagnostic confirmed that our chain length was adequate. The autocorrelation function in WinBUGS showed that dependence between posterior samples decreased at an adequate rate, therefore, we did not thin our samples.

In addition, for the model selected by DIC, we also performed 2 subsequent diagnostic analyses. First, the data was reanalyzed using uniform (0, 500) prior distributions for σ_b , $l = 1, \dots, k$. This change of priors was performed to examine how robust the results were to selection of the variance components prior. Second, for the final DIC selected model, the relocation data was also thinned to observations recorded every 3 days to assess whether there is any animal persistence (the tendency of an animal to stay in a particular location unrelated to selection of resources at that location). This resulted in 500 animal relocations.

Model Selection

To illustrate possible inferences using random effects, model comparisons were conducted at 2 levels. First, we assessed whether population-level selection effects and/or individual selection effects or neither (random use) contributed to explaining the variation in our data. The following 4 global models were fit:

1. A model with population-level effects and individual random effects with covariates ($x[s]$) NZ, NZ2, EZ, EZ2, and the 5 land-cover indicators (LC2–LC6). This model is appropriate if individual selection occurs and common population-level selection occurs across animals. This is the model described in the previous section.
2. A model similar to model 1 above but with no common population effects. This model was fit by setting all the population-level effects $\beta_l^* = 0$ for $l = 1, 2 \dots k$. This model is appropriate when individual selection occurs but there is no common population-level selection across animals (i.e., the β_{il} vary about zero).
3. A model similar to model 1 above but with no individual random effects. This model is appropriate when population-level selection occurs but animals do not vary in their selection of resource attributes. This model was fit by setting $\beta_{il} = \beta_l^*$ for all animals (i) and $\sigma_l^2 = 0$ for $l = 1, 2 \dots k$.
4. A no-selection model was fit by setting all population level effects $\beta_l^* = 0$ and all individual effects $\beta_{il} = 0$ for $l = 1, 2 \dots k$. Thus, the probability of use of every 8-km² grid cell is the same as its availability. For this model, there are no parameters to estimate, and the DIC calculation reduces to $-2\ln(\text{likelihood})$ with the likelihood defined in equation (3) with $pi(s) = 1/131$.

Second, we examined the contribution of covariate variables in the model. Because NZ on 21 June is strongly correlated with calf survival (Griffith et al. 2002), we included NZ and NZ2 in all candidate models. Thus, we investigated whether elevation (EZ, EZ2) and/or land-cover type (LC2 ... LC6) contributed to predicting the probability of use given that NZ and NZ2 were already in the model.

Results

The radiocollared calves used an area of <10,000 km² that encompassed foothill to coastal elevations (Fig. 1). Calves used all LC classes and the entire range of NDVI values.

The best-fitting global model (smallest DIC value) is model 1, which includes individual- and population-level selection (Table 1). The delta DIC for global models 1 and 4 (1,988.0) provides evidence of nonrandom use at the population- or individual level or both. Delta DIC for global models 1 and 2 (25.2) indicates that population-level selection is evident when allowing for individual differences in selection. Delta DIC for global models 1 and 3 (1,226.7) indicates evidence of individual animal variation in selection beyond population-level selection. Therefore, we conclude that selection occurred at both the population and individual levels.

Next, we examined the contribution of elevation (EZ, EZ2) and land-cover class (5 indicators in LC) to global model 1. The model with the smallest DIC value for the caribou calving ground data includes NZ, NZ2, and land-cover classes as indicators (Table 2). Because all delta DIC values >5, we select the model that includes both population and individual (random) effects for NZ, NZ2, and LC2–LC6 for further description.

Table 3 gives fitted values, β_l^* , their estimated standard errors and 95% highest probability density lower and upper bounds in columns 2, 3, 4, and 5, respectively. The midpoints of the bounds are not the β_l^* values because the posterior distributions are not symmetric (see Chen et al. 2000). Covariates with bounds not including zero are interpreted to contribute significantly to population-level selection. The average values of the $\hat{\beta}_{il}$ across animals and standard errors calculated by

$$\sqrt{\frac{\sum_{i=1}^m (\hat{\beta}_{il} - \bar{\hat{\beta}}_{il})^2}{m(m-1)}},$$

where m is the number of animals, are given in columns 6 and 7, respectively, for comparison.

Population-selection parameter estimates ($\hat{\beta}_l^*$; column 2, Table 3) are similar to the average of the individual-selection parameter estimates (average $\hat{\beta}_{il}$; column 6, Table 3) because the individual-selection parameters β_{il} are constrained to have means β_l^* in the random-effects model. If a separate model for each animal had been fit without the random-effects constraint, the averages likely would have differed more from the estimated population-level effect. The standard errors of the average individual-selection

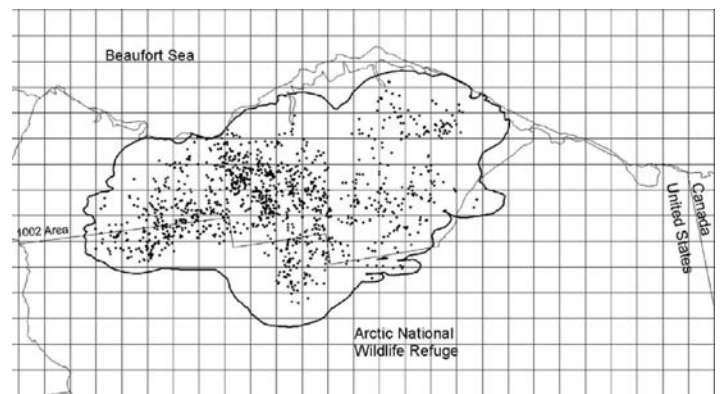


Figure 1. Distribution of relocations of radiocollared calves of the Porcupine caribou herd on the North Slope of the Brooks Range and Arctic coastal plain in Alas., USA, 1–24 June 1994. Grid size is 8 km². Solid line is the outer perimeter of all daily population-level 99% utilization distributions.

Table 1. Global model-selection results.

Model	DIC	Delta DIC	Rank
(1) Population and individual random effects including all covariates	10385.3	0.0	1
(2) Individual effects, no population effects	10410.5	25.2	2
(3) Population effects only (all covariates) no random effects	11612.0	1226.7	3
(4) No population effects, no random effects, the no selection model	12373.3	1988.0	4

Table 2. Model-selection results for covariates in population effects.

Model	DIC	Delta DIC	Rank
Population effects (random effects included)			
NZ, NZ2, LC2-LC6	10378.0	0.0	1
NZ, NZ2,EZ,EZ2, LC2-LC6	10385.3	7.3	2
No population effects of covariates	10410.5	32.8	3
NZ,NZ2	10418.9	40.9	4
EZ,EZ2, NZ,NZ2	10434.7	56.7	5

parameter estimates (column 7) are misleadingly small (10–60% as large as the population-selection parameter standard errors [column 2]) because this approach does not incorporate differing numbers of relocations among animals. As a result, researchers using the average of individuals based standard errors (column 7) are likely to conclude population-level selection for some variables that are not warranted.

Individual caribou selection parameter estimates, $\hat{\beta}_{ih}$, are centered near zero for covariates EZ, EZ2, LC2, LC3, and LC4 (Fig. 2). Thus, the DIC results indicating EZ and EZ2 do not contribute to predicting probability of use are confirmed by the box plots of individual-selection parameter estimates. Because wet sedge was used as the land-cover reference type, interpretations of the parameter estimates for LC2–LC6 are relative to that land-cover type. Thus, we infer that moist sedge (LC2), herbaceous tussock tundra (LC3), and shrub tussock tundra (LC4) are selected about the same as wet sedge, while alpine (LC5) and sparsely vegetated (LC6) are selected less than wet sedge. Furthermore, the variability in selection for moist sedge plots (LC2) and sparsely vegetated (LC6) is large relative to the variability in selection of other land-cover types. The differences in variability are also reflected in the estimated variances, $\hat{\sigma}_i^2$, which were 3.237, 2.108, 6.540, 4.958, 3.783, 0.509, 2.171, 1.676, and 72.82, respectively, for the variables as arranged left to right in Fig. 2. The 5 outliers in LC6 were the only 5 animals that used sparsely vegetated plots even though this cover type made up 18 of the 131 available cells and these animals caused the large variance for LC6. The 2 animals with low outliers for the NZ parameter estimates moved less than others and used cells with lower-than-average values of NZ.

The model can be used to depict the probability of use of the 131 cells (Fig. 3). In our example, random use would predict a probability of use of 0.008 (1/131), but the model predicts that use of cells varies from less than one-quarter to 3 times as great as expected on the basis of random use.

The results of the 2 diagnostic analyses, use of uniform variance component priors to assess sensitivity to choice of prior and thinning the data to relocations every 3 days to assess the impact of relocation persistence, did not change the inferences concerning the significance of the cell attributes in the model. That is, the β_i^* significant in the original analysis were significant in each of the 2 diagnostic analyses. Using the uniform prior for the random-effect variances, the β_i^* were 3.426, -3.075 , -0.759 , -2.06 , -0.567 , -1.983 , and -13.330 , and the estimated variances, $\hat{\sigma}_i^2$, were 3.497, 2.314, 7.018, 5.316, 3.927, 0.567, 2.355, 2.505, and 96.19. Thus, the choice of prior for the random-effects components made little difference in estimated parameters and had no impact on

inferences. Using the thinned data, the β_i^* were 1.901, -1.970 , -0.572 , 0.227, -0.287 , -1.404 , and -1.932 , and the estimated variances, $\hat{\sigma}_i^2$, were 0.028, 0.006, 1.800, 1.236, 1.377, 0.041, 1.509, 0.154, and 0.764. The β_i^* values were closer to zero because less data was available to offset the prior, and the coefficient LC3 changed sign but still was not significantly different from zero, so inferences concerning selection remain unchanged. In addition, the variance component estimates, $\hat{\sigma}_i^2$, for the thinned data were much smaller than those for the full data set because thinning removed many of the outliers in the data. Overall, the alternate priors and thinned data analyses did not indicate a problem with prior sensitivity or animal persistence that would influence inferences made for the original analysis.

Discussion

Random-effect models allow individual heterogeneity through the data model and population inference through the hyperparameters. Information in the data is shared between the data model and the parameter model. For example, for those individuals with few observations, parameters would be poorly estimated in an individual model only using data for that animal. In the random-effects model, estimates of individual effects contribute to population-level estimates, which in turn contribute to individual-effect estimates through the parameter model. This feedback loop allows individuals with different numbers of relocations to share information with the data model in a way that treats each individual equally but numbers of relocations differently. Thus, this information sharing provides a weighting scheme for different numbers of relocations per animal in the data to influence population-level parameter estimates.

Bayesian credible intervals have a more natural interpretation than classical confidence intervals. For example, the inference from the 95% credible interval for the coefficient for NZ is that the true value of this parameter lies within (2.544, 4.207), with probability 0.95. Within classical or frequentist statistics, such a statement is invalid because the parameters are assumed to be fixed.

Several realistic extensions of the model presented are possible. First, a persistence parameter, as proposed in Ramsey and Usner (2003), may be included in our model if animals have a tendency to linger in the same grid cell for more than 1 relocation period. Second, additional covariance structure, rather than independence, may be added to the model if animals do not behave independently but move in groups. Finally, different choice sets of available grid cells (see Cooper and Millspaugh 1999) for each individual animal may be used rather than assuming that all grid cells were equally available to all animals by adjusting $a_i(s)$ in equation (1).

Although the power of a test is not a Bayesian issue, users are

Table 3. Population-selection parameter estimates and standard errors.

Covariate	Population selection parameter estimate	Standard error	95% HPD interval lower bound	95% HPD interval upper bound	Average value of individual selection parameter estimates	Standard error of average individual selection parameter estimates
NZ	3.376	0.427	2.544	4.207	3.384	0.238
NZ2	-3.023	0.368	-3.752	-2.318	-3.027	0.209
LC2	-0.747	0.305	-1.336	-0.162	-0.749	0.182
LC3	-0.202	0.225	-0.628	0.237	-0.202	0.042
LC4	-0.557	0.300	-1.130	0.039	-0.557	0.124
LC5	-1.820	0.490	-2.857	-0.950	-1.822	0.060
LC6	-11.772	4.081	-19.980	-4.714	-11.905	0.413

likely to ask what sample sizes are needed to estimate population-level effects and individual effects using the random-effects model described. The model presented is sample-size specific and does not depend on large sample approximations. However, the ability to estimate population-level effects will be determined by the number of animals in the data and, similarly, the number of relocations per animal determines the quality of the estimation of individual effects. For example, the 1 caribou in our data set with only 3 relocations has individual-effect values very close to the population-level effects because 3 observations do not provide sufficient information to model the effects for this individual well. Thus, in model-selection comparisons, the quality of parameter estimates and their standard errors depend on the number of animals and the number of relocations per animal. While the model fit well for the caribou data analyzed and differences in models were detected with the 76 animals and 1,269 relocations described with ≤ 21 relocations per caribou, we concur with

Allredge and Ratti's (1986) recommendation to have ≥ 20 animals with ≥ 50 independent relocations per animal.

We emphasize that the inclusion of all biologically relevant independent variables in discrete-choice models is desirable. For simplicity, we considered only 3 habitat variables in our model. Apparent differences between the distribution of observations and modeled mean probability of use may or may not be explained on the basis of modeled variables. For example, the cloud of relocations in the northeast quadrat of our analysis space is not well represented in the predicted mean probability of use. Low predicted use of the northeast quadrat was caused by very low values for NZ, and only 11 of the 76 animals used the area. Conversely, predicted high probability of use in the southeast quadrat and western end of our analysis space is not congruent with the density of observations in these areas. In this latter case, we may have failed to include relevant variables, or our resampling of habitat to a relatively coarse 8-km² resolution may have reduced model performance.

Management Implications

The objective of most resource-selection studies is to better understand selection at the population level to address management concerns. Population-level inference usually includes such quantities as some measure of "average" selection and a measure of variability in selection among animals. Both pieces of

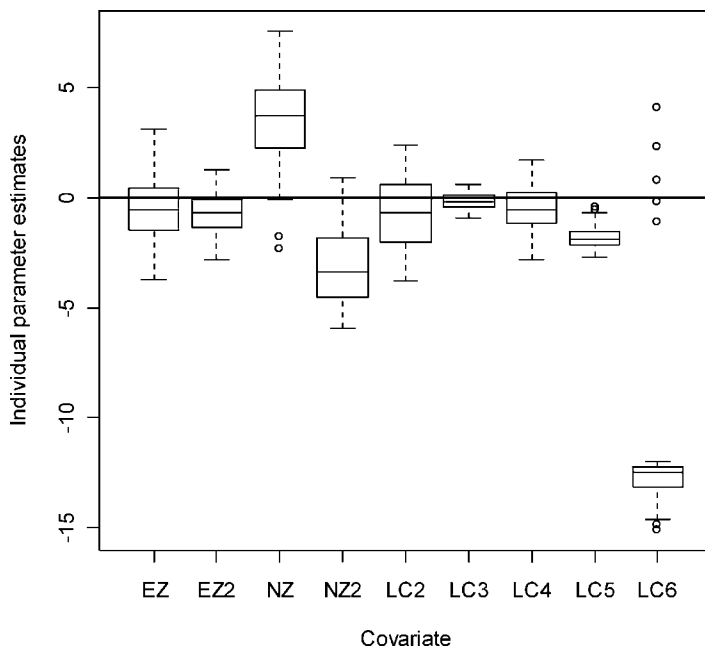


Figure 2. Boxplots of individual parameter estimates for each covariate. Boxes indicate first and third quartiles with median shown as a line in the box. Dashed lines extend to ± 1.5 times the interquartile range from the quartiles. Outliers are shown as individual points.

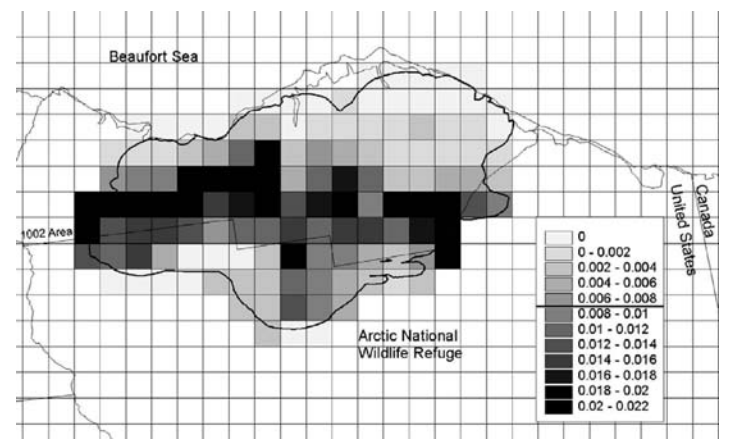


Figure 3. Predicted mean probability of population use of 8-km² cell ($p(s)$ using β_i^*) by female calves of the Porcupine caribou herd, 1–24 June 1994, North Slope of the Brooks Range and Arctic coastal plain, Alaska, USA. The horizontal line in the legend indicates random-use probability. Darker cells have higher estimated probability of use.

information are necessary for determining what management applications may be necessary for a particular objective. Examining the average selection of a particular resource provides only half the information a manager needs.

There was substantial heterogeneity in habitat conditions (e.g. snow cover, timing of vegetation green-up) and calving ground location for the Porcupine caribou herd during 1983–2001 (Griffith et al. 2002). Our example analysis of a single year from this long-term series captures neither the climate-induced trend in habitat nor the multiscale heterogeneity in habitat selection that was present (Griffith et al. 2002). Thus, our results reported here should not be used to formulate explicit management recommendations on the Porcupine caribou herd. We can, however, examine the information that managers can gain from this analysis.

Examination of Fig. 2 illustrates that on average, Porcupine caribou tend to select the wet sedge landscapes, but there is a large amount of variability among animals; many animals actually prefer the other land-cover classes more than wet sedge. Hypothetically, if managers wanted to identify quality habitat from this example, based on the population-level selection coefficients (Table 3), they might decide that wet-sedge habitat is high quality. But, examination of the variability shows that a substantial section of the population may not select wet sedge habitat over the other classes. Or, managers may want to examine the moist sedge category and note that “on average” it is selected at a lower rate than wet sedge, but there are a substantial number of animals that do, in fact, select moist sedge with higher frequency.

Due to an ever increasing level of technology, managers are employing studies using telemetry of individual animals to make population-level management decisions. The Bayesian analysis illustrated herein is specifically designed to provide managers with

the 2 components of population-level selection inference, average selection and measures of selection variability among animals. Using these telemetry data to fit a single model for all individuals; i.e., using relocations as the sampling unit, may lead to false inference due to inherent individual heterogeneity. Models for individual animals, on the other hand, do not provide population-level inference, and averaging individual model coefficients across animals may underestimate error when different numbers of relocations were made on animals. Hierarchical models provide a compromise and possess the benefits of both.

Bayesian methods were used here to illustrate a hierarchical model for assessing population-level selection. These methods allow more complex models for resource selection than have been used in the past. Many researchers, however, are not likely to be familiar with Bayesian methods and MCMC computation in particular, although they are rapidly becoming staples of ecological research. Therefore, the use of these methods will require researchers to study Bayesian methods and become familiar with related software. However, those using the more complex models that may be fit with Bayesian methods are likely to be rewarded with a greater understanding of the factors influencing habitat selection and thus, be better equipped to make management decisions that will produce desired results.

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Appendix A. Format of the WinBUGS Data Input File.

```
list(
N = 1269, #number of animal relocations
Na = 76,  #number of animals
Ns = 131, #number of grid cells
K = 9,    #number of covariates
```

```
z=structure(.Data=c(#EZ,EZ2,NZ,NZ2,LC2,LC3,LC4,
LC5,LC6 for each grid cell
-0.948043, 0.898785, -0.775481, 0.60137, 0, 0, 0, 0, 1,
-0.936456, 0.876949, -1.09195, 1.19236, 1, 0, 0, 0, 0,
-0.94418, 0.891477, -0.986463, 0.973109, 1, 0, 0, 0, 0,
:
3.77575, 14.2563, -0.669989, 0.448886, 0, 0, 0, 0, 1,
2.86035, 8.18157, 0.0684484, 0.00468519, 0, 0, 0, 0, 1),
.Dim=c(131,9)),

x=structure(.Data=c(#animal number, grid cell location for all
animal locations
1, 38,
1, 55,
1, 69,
2, 12,
2, 27,
2, 2,
:
76, 71,
76, 36,
76, 71), .Dim=c(1269,2))
)
```

Appendix B. WinBUGS Program.

```
#Discrete Choice random effects (one covariate)
model
{
# i is the index for animal, i = 1 , 2, ... , Na
# s is the index for the location cell, s = 1, 2, ... , Ns
# j is an index across all animal relocations, j = 1, 2, ... , N
# x is a matrix of all animal locations
#   with column 1 = animal number, column 2 = cell number
# z is a matrix of all cells
# with column 1 = cell number, remaining columns are covariate
# values for each cell
# K is the number of covariates
# if only discrete resources, K = number of resources
# (h-1 indicators + ln avail)
# Normalize continuous covariates
# (not ln avail in discrete resources)

# Likelihood specification
for(j in 1:N){
  x[j,2]~dcat(p[x[j,1],1:Ns])
}

# Link specification
for(i in 1:Na){
  for(s in 1:Ns){
    eprod[i,s]<-exp(inprod(z[s,],abeta[i,])+lnavail[s])
    p[i,s]<-eprod[i,s]/sumeprod[i]
  }
  sumeprod[i]<-sum(eprod[i,])
}
```

```

# Prior specification
for(i in 1:Na){
  for(k in 1:K){ abeta[i,k]~dnorm(beta[k],tau2[k]) }
}
for (k in 1:K){
  beta[k]~dnorm(0.0, 0.01)
  tau2[k] ~ dgamma(0.01, 0.01)
  sig2[k] <- 1/tau2[k]
}

}# End model loop

```

Appendix C. Definition of Deviance Information Criteria (DIC).

$$\text{DIC} = \text{Dbar} + \text{pD} = \text{Dhat} + 2^* \text{pD},$$

where Dbar is the posterior average of $-2*\ln(\text{likelihood})$ across MCMC steps, Dhat is the value of $-2*\ln(\text{likelihood})$ using posterior average of parameters across MCMC steps and pD, called the “effective number of parameters” is $\text{pD} = \text{Dbar} - \text{Dhat}$. If there are no parameters in the model, then $\text{Dbar} = \text{Dhat}$ so $\text{pD} = 0$.

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